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Turbidites and Benthic Faunal Succession in the Deep Sea: An Ecological Paradox?

David K. Young, Michael D. Richardson*, and Kevin B. Briggs

Abstract: Characteristics of benthic faunal succession following turbidity flows in the deep sea will vary according to the composition of turbidite materials, the spatial scales of deposition, the structure of initial benthic communities, and the frequency of depositional events. Despite a number of uncertainties regarding these effects, we make several generalizations in order to stimulate research on successional responses of benthic fauna to such episodic events. We find no support for a hypothesis formulated on the speculation by Heezen et al. (1955) that there should be, "... a high [positive] correlation between nutrient-rich turbidity current areas and a high standing crop of abyssal animals." There is no definitive evidence for the extensive 'mining' of deeply deposited sediments reported by Jumars and Gallagher (1982) as being a foraging strategy for deposit-feeding benthos in turbidite sediments. The time for complete recovery of the benthic fauna following an episodic deposition of material on the scale of a turbidity flow is postulated to be hundreds to thousands of years. If viewed as a matrix of dynamic events, the effects of turbidity flows on abyssal fauna are on larger spatial and longer temporal scales than most other deep-sea disturbances and therefore provide the biological framework upon which many of the smaller and shorter term effects are superimposed. In interpreting and reconstructing causes for distributions of deep-sea organisms, benthic ecologists should incorporate a similarly holistic view (i.e., the turbidity current paradigm) as sedimentologists in order to better understand how the abyssal benthic fauna has adapted to episodic disturbances over geologic time.

Introduction

Results from early deep-sea explorations (e.g., Agassiz 1892; Mortensen 1938; Bruun 1953) provided the scientific framework for the views of Bruce Heezen, Maurice Ewing, and Robert Menzies that turbidity currents play a potentially significant role in abyssal productivity. In speculating about the role of turbidity currents in the nutrition of deep-sea benthos, they state that there should be, "...a high [positive] correlation between nutrient-rich turbidity current areas and a high standing crop of abyssal animals" (Heezen et al.1955, p.180). This statement, considered herein as a testable hypothesis, has never been critically examined. In this paper, we test the hypothesis based on results from recent research that quantifies the relationships between organically rich turbidite deposits and biomass in deep-sea fauna.

Jumars and Wheatcroft (1989) state that turbidite sediments should be important sources of organic enrichment of deep-sea fauna but note that successional sequences and times for recovery from the initial disturbances are unknown. Jumars (1993) later questions what successional information could be resolved from such 'unsteady sequences' as turbidites. He suggests that, "A great deal more will be learned for biology when stratigraphers become braver in interpreting jumbled sedimentary sequences complete with erosive gaps and turbidites" (Jumars 1993, p. 301). We agree with Jumars' suggestion. In the present paper, we use the data from well-studied abyssal plains to interpret characteristics of faunal succession following episodic depositions of sediment by turbidity currents in the deep sea. We recommend areas of research requiring further attention and suggest that a new viewpoint needs to be taken by benthic ecologists who undertake such work.

Whereas this paper focuses on animal-sediment relationships in turbidite deposits, we acknowledge the research showing a strong positive correlation among pelagic sedimentation rates, particulate organic carbon flux, and bioturbation rates in parts of the abyssal ocean dominated by pelagic deposition (Jahnke & Jackson 1992). The low biomass of abyssal benthos is recognized to result from the extremely low fluxes of organic matter reaching the great depths of the deep sea (reviewed by Rowe 1983). In pelagic sediments, increases of organic carbon flux from water column transport of detritus to the abyssal seafloor correlate with higher bioturbation rates and greater depths of biogenic reworking (Trauth & Sarnthein 1997). High rates of organic flux are also positively correlated with higher abundance, greater biomass, and larger mean body size of deposit-feeding benthic fauna in the deep sea (Smith 1992). Benthic standing stock is less well correlated with percent organic matter than with organic flux rates, as most organic matter found below the upper few centimeters is refractory in nature and of little nutritional value (Richardson & Young 1987). Deposit-feeding megabenthos, though less abundant than the smaller macrobenthos, dominate spatial and temporal scales of bioturbation, thereby controlling diffusion and advection of particles and solutes, which affect rates of sediment diagenesis (Wheatcroft et al. 1990).

Background

A SHORT HISTORY OF DEEP-SEA BENTHIC INVESTIGATIONS

The understanding of deep-sea biological processes has evolved as scientists have obtained new information on biotic interactions and rates of deep-sea processes as a result of technological advances in seafloor experimentation and of sampling this remote environment. Changes in our understanding of the deep-sea fauna may be viewed in terms of the following significant events.

Despite rare collections by a few scientists showing that life existed in abyssal ocean depths, the deep sea was assumed to be a biological desert during times prior to the *Challenger* expedition (pre-1872). This "azoic theory," usually attributed to Edward Forbes, was reviewed in detail by Mills (1983). Inaccessibility of the deep sea fostered the predominant opinion of an environment in which perpetual darkness, lack of plants, low temperature, and high pressure precludes the existence of life.

Extensive sampling of diverse deep-sea fauna during the H.M.S *Challenger* expedition (1872–1876) refuted the azoic theory. From analyses of these samples emerged a new view of the deep sea being inhabited by relict fauna (i.e., ancient life forms that have changed little over geologic time) and of the abyssal ocean as a "refugium" where processes proceed at very slow rates (reviewed by Menzies & Imbrie 1958). Charles Wyville Thomson reported on qualitative collections from this first deep-sea expedition on a global scale, showing similarities of the abyssal fauna (i.e., "cosmopolitan" species) among ocean basins (Thomson 1878).

The intensive period of international, worldwide expeditions during the 1950s–1960s was characterized by the first quantitative benthic sampling of the deep sea (reviewed by Mills 1983). A picture developed of a sparse, though diverse and speciose, fauna sustained by a slow rain of detritus, where changes occur very slowly and biota are sensitive and susceptible to environmental change (i.e., "biologically accommodated") (Sanders 1968). Deep-sea species were seen as members of a fragile fauna that evolve slowly, grow slowly, and are long-lived.

Benthic colonization experiments during the 1970s–1980s, beginning with the serendipitous "Alvin lunch" experiment, fostered a new understanding of the rates of microbial and other benthic processes in the deep sea (reviewed by Gage & Tyler 1991). The early in situ experiments revealed rates of years for the benthic recolonization of trays of azoic sediments by opportunistic species (Grassle 1977). Subsequent experimental manipulations via mechanical disturbances and organic enrichments demonstrated that recolonization may only require weeks to months and suggested that trays may cause artificial conditions that impede rates of recolonization (Grassle & Morse-Porteous 1987; Smith 1992). The short-term nature of these experiments precluded assessment of the time required for the fauna to reach equilibrium (prior to disturbance) conditions.

A more temporally and spatially dynamic picture emerged from the sediment trap measurements and observations of "falls" of organic matter in the 1970s–1980s. Naturalists have often observed that organic material such as wood, seaweeds and seagrass are rapidly colonized and often eaten by deep-sea fauna (reviewed by Gage & Tyler 1991). Sediment trap measurements pioneered by Honjo (1978) and others revealed pulsed, seasonal inputs of organic matter from algal blooms, which are rapidly fed upon by specialized surface deposit-feeders. Observations by remote video (Isaacs 1969) and research submersibles (Smith 1986) showed that "opportunistic" scavengers (bathypelagic fish and benthic invertebrates) rapidly congregated on and fed upon fish carcasses.

In 1977 there was an unexpected discovery of large, chemoautotrophic faunas associated with deep-sea hydrothermal vents (Corliss et al. 1979). The vent fauna is characterized by low diversity, rapid rates of colonization and very high growth rates (Lutz et al. 1994). Such observations led John Gage to state (Gage 1991, p.87), "...low reproductive production, slow growth and great age is by no means the general rule in the deep sea." The commonly held viewpoint today is that vent-type communities may occur wherever sufficient organic matter can create the reducing conditions required for chemoautotrophic production in the otherwise oxic, food-limited deep sea (Gooday & Turley 1990). Vent communities can be considered as one of a "parallel" grouping of marine fauna (Gage & Tyler 1991) associated with other sources of reduced compounds, such as submarine seeps, organically rich reduced sediments, whale carcasses, and sunken cargoes. The reduced compounds serve as energy sources for chemolithoautotrophic bacteria, which, in turn, provide food for this fauna (reviewed by Young & Valent 1997).

Episodic Deposition in the Deep Sea

We re-evaluated our understanding of deep-sea biological processes when recently confronted with having to assess the potential impact of benthic succession following the disposal of dredged material on the abyssal seafloor (Young & Valent 1996). There was no existing body of knowledge with which to assess this problem directly (reviewed by Valent & Young 1995). We therefore made the analogy between sudden deposition of dredged material on the abyssal seafloor and episodic deposition of sediment by turbidity flows in order to assess the ecological effects and the time for recovery of an abyssal fauna affected by such an event (Young & Richardson 1998).

Relationships of Episodic Depositional Events to Biological Processes in the Deep Sea

Episodic depositional events caused by localized slides or slumps, such as those associated with the 1929 Grand Banks earthquake (Heezen & Ewing 1952), and with large-scale turbidity flows have produced the abyssal plains of the world's oceans (Weaver et al. 1987). It is clear that deep-sea fauna have had to cope with such periods of destruction and recovery from episodic depositional events over the course of geologic time, particularly during periods of glacially lowered sea-level (Bowles et al. 1998). Young and Richardson (1998) conclude that the time for recovery of the benthic fauna from episodic depositions on the scale of a turbidity flow, including adjustment to the changed sedimentary and geochemical environment, will vary according to the sedimentary characteristics of the turbidite material itself, and also to the spatial scales (including areal extent and thickness), the composition of the initial benthic community, and the frequency of the depositional events.

Individual turbidite deposits resulting from turbidity flows may have volumes as large as 120 km^3 (Weaver et al. 1987) and depths up to 100 m, although thicknesses of centimeters to meters are more common, especially at the distal ends far from continental landmasses (Pilkey 1987). Spatial scales are generally related to basin morphologies, bathymetric gradients, and distances from continental margins, and are dependent on quantities of source material and the magnitude of the stimulus triggering the depositional event (Gorsline 1980).

Time periods between turbidity currents producing turbidite layers in the deep sea are quite variable. Various indices, such as times between cable breaks and stratigraphic markers (ash layers, faunal changes, and radioisotopic dating), have been used to determine recurrence intervals for turbidity flows. Piper and Normark (1983) report an inverse relation between layer thickness and the frequency of depositional events in ancient turbidites. This inverse relationship is noted for turbidites generated by both seismic and sedimentological processes. The sparse data on published flow periodicities are summarized in Table 1 for events from the Holocene and earlier ages.

There are relatively few observations or measurements of bioturbation in locations of the turbidity flows referenced in Table 1. For the Congo Submarine Canyon with frequent turbidity flows, Heezen and Hollister (1971, p.301) note that the time for benthic animals "...to track newly deposited mud is measured in weeks and not in years." Areas of the deep sea that are subject to frequent depositional events are apparently characterized by benthic fauna that have adapted over time to these periodic disturbances (Aller & Aller 1986). In the case of the San Pedro and Santa Monica basins, where anoxic and hypoxic conditions prevail, there are no living macrofauna and sediment sequences are undisturbed by bioturbation (Gorsline & Emery 1959). For the Carpathian Flysch Formation, Sujkowski (1957) reported fossil evidence of allochthonous, broken, shelly fossils within turbidites that were deposited at slope depths on an average of once every 4,000 yr. Graptolites and pteropods are common in the pelagic layers that are presumed deposited at time intervals between the turbidites.

Notable exceptions to the paucity of information about bioturbation in turbidite locations are the Cascadia Channel-Abyssal Plain in the Northeast Pacific (Griggs et al. 1969), the Madeira Abyssal Plain in the Northeast Atlantic (Weaver et al. 1987), and the Venezuela Abyssal Plain in the Caribbean Sea (Richardson et al. 1985). By examining published evidence from these turbidite sedimentary provinces, in which depositional and bioturbation rates have been studied, we hope to gain a better understanding of the spatial and temporal scales of change and recovery of a deep-sea fauna from the impact of episodically deposited sediment in abyssal depths.

Much of the surface sediment of the GME area is composed of a recent turbidite layer (Wilson et al. 1985) characterized by having no recognizable veneer of overlying pelagic sedimentation and minimal bioturbation (Table 3), which is limited to surficial sediments (Jarvis & Higgs 1987; Thomson et al. 1987). This turbidite layer resulted from a turbidity flow that occurred about 1,000 yr before present (Thomson & Weaver 1994). Huggett (1987) reports that the turbidite layer could be distinguished from adjacent abyssal pelagic sediment on the basis of surface "Lebensspuren" (i.e., life traces), suggesting basic differences in faunal foraging behavior between the two sedimentary provinces. The dominant lebensspuuren on the turbidite sediments are meandering traces attributed to mobile foragers and small spokes produced by sessile fauna; whereas, the pelagic sediments are characterized by irregular traces attributed to mobile foragers and medium-size spokes produced by sessile fauna. Huggett (1987) postulated that these different foraging strategies result from differences in near surface organic carbon (0.12–0.15% organic carbon in pelagic sediments versus 0.25% organic carbon in the turbidites) (Table 2). He also suggested that the turbidite sediments are too young (1,000 yr) to have been totally reworked by benthic fauna.

Thurston et al. (1994) report smaller size megafauna with a lesser overall standing crop and lower biomass from a site in the GME area of the Madeira Abyssal Plain (centered at 31°15' N, 25°25' W at 5,440 m water depth) compared with a site in the Porcupine Abyssal Plain (PAP) that was unaffected by recent turbidite flows (centered at 48°50' N, 16°30' W at 4940 m water depth) (Table 2). Thus, no increase in benthic biomass is found at the GME area that could be attributed to an increase in organic carbon in the surface turbidite layer. These findings are contrary to the hypothesis of Heezen et al. (1955). Rice (1997 personal communication) hypothesizes that a higher quality of phytodetritus at the PAP site could account for the differences of benthic biomass between sites, but reports (Rice et al. 1994) that a significantly higher flux of suspended matter has not been measured at the PAP site compared with the GME site. Accumulation rates for pelagic sediments in the GME area vary between 0.1 and 1.0 cm kyr⁻¹ (Weaver & Rothwell 1987), so it is apparent that there has been insufficient time for pelagic sedimentation to cover the turbidite deposit, especially given surficial mixing of sediments by benthic fauna. In noting the shallowness of the surface mixed layer, Thomson and Weaver (1994, p.3) state that, "...a deeper mixed layer might have been expected if this [more organic matter] had attracted higher biological activity."

Thurston et al. (1994, p. 1344) state that it was 'unlikely' that residual effects of the turbidite deposit are affecting the megafaunal community at the GME area. Evidence for long-term effects of turbidity flows upon abyssal animal communities, as discussed by Young and Richardson (1998), suggest that low densities and biomass of megafauna at the GME site could be caused by such an episodic event even after 1,000 yr. In fact, the small individual sizes and overall low biomass of megafauna at the GME site likely result from residual effects of the relatively recent turbidity flow in this area of the Madeira Abyssal Plain. This conclusion, though discounted by Rice (1997, personal communication), remains as the most parsimonious explanation for the observed results.

Venezuela Abyssal Plain

The turbidite site is located in the central Venezuela Abyssal Plain (13°45' N; 67°45' W) of the Caribbean Sea at the distal end of ponded turbidity flows from the adjacent Colombia Basin, which originated at the Magdalena River Delta (see Table 1). These turbidity flows deposited layers of organic-rich (up to 1.55% organic carbon) terrestrial materials onto an organic-poor pelagic sediment (Table 2).

The sediment profiles at the turbidite site are characterized by a largely undisturbed, 14-cm-thick turbidite layer possessing different properties than the layers of highly bioturbated, pelagic deposits above and below it (Young & Richardson 1998). The turbidite layer exhibits typical graded bedding and contains sediment of coarser grain size and lower porosity than the pelagic layers (Briggs et al. 1985). The organic carbon content of the thickest turbidite layer, though variable, is very high for deep-sea sediment (Waples & Sloan 1980). The rapid deposition of sediments associated with the turbidite flow apparently produced "...a hiatus in bioturbation activity," and preserved intact gradients of sediment properties in buried pelagic layers which were "...created and maintained by past biological activity" (Richardson et al. 1985). X–radiograph profiles of the interface between the turbidite layer and the buried pelagic layer (Briggs et al. 1985) exhibit vertical failed escape burrows, suggesting that motile burrowers attempted, without success, to reach the new sediment surface.

The sedimentation rate of pelagically derived material at the Venezuela Basin turbidite site following the episodic turbidity flow event was 7.2 cm kyr^{-1}, as determined by activity profiles of uranium and thorium series isotopes (Cole et al. 1985). This rate suggests that the latest turbidity flow event occurred about 2,000 yr ago. Radionuclide profiles show highest biogenic mixing rates (900 cm^2 kyr^{-1}) for the upper 4–8 cm of the pelagic layer overlying the turbidite layer (Li et al. 1985). As with the example from the Madeira Abyssal Plain (Huggett 1987), the Lebensspuren from the turbidite province of the Venezuela Abyssal Plain are markedly different from those of adjacent sedimentary provinces (Young et al. 1985), with lower diversity of types and a higher concentration of sedentary verses mobile forms compared to pelagic and hemipelagic sites.

The faunal differences between the turbidite and the other two provinces within the Venezuela Basin are striking. Trawl data presented by Briggs et al. (1996) indicate that in comparison with the pelagic and hemipelagic provinces, the turbidite province has lower species diversity, lower species richness, and fewer deposit feeders. Furthermore, sponges and holothurians dominate the trawl catches of the turbidite province, in contrast to the mollusks, decapods, and fishes that dominate at the adjacent provinces.

Biochemical analyses (Baird & White 1985; Shaw & Johns 1985) show that the layered turbidite sediment of the Venezuela Abyssal Plain contains labile organic compounds that are nutritious to deposit feeders. The biomass of meiofauna and macrofauna (Richardson & Young 1987) and of megafauna (Briggs et al. 1996) is low in relation to the organic matter potentially available to consumers at this site (Table 2). As with the examples from turbidite deposits of the Cascadia Channel and those of the Madeira Abyssal Plain, the hypothesis that nutrient enrichment by turbidity currents results in a high standing crop of abyssal animals (Heezen et al. 1955) is not supported by data from the turbidite province of the Venezuela Basin.

Benthic Faunal Succession in Deep-Sea Turbidites

If an analogy with shallow-water, benthic successional stages (sensu Rhoads et al. 1978) is applicable, early benthic 'pioneers', or opportunists, in the deep sea should be followed by a benthic fauna that feeds at greater depths within the sediment. In shallow-water marine benthic environments, equilibrium assemblages comprise long-lived, large, deposit-feeding individuals that reestablish themselves only after several years following a major disturbance (Rhoads & Germano 1982). Young and Richardson (1998) speculate that the time to reach the stage of an equilibrium benthic assemblage in deep-sea turbidite deposits is on the order of hundreds to thousands of years. Given sufficient time, the resulting equilibrium benthic assemblage should consist of more abundant and larger animals that

have higher bioturbation rates and deeper mixing depths than the fauna that existed prior to the depositional event.

Sequences (A) and (B) of Fig. 2 show two hypothetical scenarios for benthic faunal succession of organically rich turbidite depositions in the deep sea. Both scenarios assume sufficiently thick depositions that destroy the benthic fauna by burial (Young & Richardson 1998), while the resulting relict burrows are preserved in situ as described by paleontologists (see overview by Seilacher 1991).

Sequence (A) of Fig. 2 presumes that the turbidite layer is completely mixed with the overlying pelagic sediments by benthic fauna. This scenario shows that the deep-burrowing benthic fauna has extensively "mined" the turbidite layer assuming that the energy expended to make deep burrows has metabolically repaid the cost of making them (sensu Jumars & Wheatcroft 1989). The stratigraphic result of this activity (final member of sequence A, Fig. 2) is that the turbidite layer is destroyed and only those relict burrows below the depth of deepest biogenic reworking are preserved. This end-member stage is a likely result predicted by optimal foraging theory, assuming that no hiatus prevents the recruitment by benthic fauna and that sufficient time is available to completely rework the turbidite layer. Such a stratigraphic result, however, has not been seen in any of the turbidite sequences reviewed in this paper (see Table 1 and Table 3).

Sequence (B) of Fig. 2 presumes that a delay in benthic faunal recolonization of the turbidite layer results in an initial hiatus of bioturbation following turbidite deposition. The preservation potential of sedimentary event layers, dependent upon competing processes of sediment reworking and rates (and depths) of deposition, therefore requires that a time-lag (long initial rest period, sensu Wheatcroft 1990) be introduced. The large areal extent of influence by turbidites and the slow modes of faunal recruitment can reduce the rates of recolonization of new substrata, as discussed by Young and Richardson (1998). A time lag can also be the result of insufficient oxygen to support aerobic respiration, particularly following episodic introductions of organically rich material (Jahnke 1998). Savrda and Bottjer (1991) show that laminated strata in fossil turbidite deposits are preserved during periods of anoxia and that higher bioturbation activities and deeper biogenic reworking of subsequently deposited sediment take place after oxygenation of bottom water is reestablished. The past presence of near-surface reducing conditions in turbidite sediments of the Venezuela Abyssal Plain is revealed by a thin, crusty iron-rich layer between the surficial pelagic and buried turbidite layers (Briggs et al. 1985). The turbidite layer with volcanic ash from the Madeira Abyssal Plain (Table 3) shows a similar hiatus of biogenic mixing by benthic fauna. The stratigraphic result of a delay in benthic faunal recolonization (see final member of sequence B, Fig. 2) is a higher probability of preservation of turbidite and pelagic layers. The resultant stratigraphy, of layered sequences of unmixed layers interspersed with bioturbated layers, is what is most commonly observed in deep-sea turbidite sediments (Piper & Stow 1991) and in turbiditic sedimentary rocks (Sepkoski et al. 1991).

Conclusions and Speculations

We do not find support for the hypothesis formulated from the speculation of Heezen et al. (1955) that there should be, "...a high [positive] correlation between nutrient-rich turbidity current areas and a high standing crop of abyssal animals." We also find little evidence for extensive deep deposit "mining" of turbidite sediments suggested by the optimal foraging theory (Jumars & Gallagher 1982). In fact, the mere existence of layered stratigraphic sequences so commonly observed in deep-sea turbidites and turbiditic sedimentary rocks depends upon incomplete sediment mixing.

We suggest that evoking the models of "equilibrium" and successional stages for the benthic fauna of turbidite deposits in the deep sea is not heuristic and may not be appropriate. In considering the high unpredictability of turbidite currents, by definition, deep-sea benthos may not often have sufficient time to adapt to such episodic disturbances, as have shallow-water species. Perhaps viewing benthos of deep-sea turbidite deposits as "relics of former disasters" (sensu Johnson 1972) is more testable and inherently useful than considering benthic succession in these sediments as leading to equilibrium communities. As Jumars (1993, p. 301) asked, "Do geological old segments of the record of unsteady sedimentation [as turbidite sequences] suggest a fauna that was more poorly evolved to deal with unsteady sedimentation?" Our analysis of observations reported in this paper is supportive of this suggestion.

The turbidity current paradigm (Kuenen & Migliorini 1950) produced a dramatic change in the sedimentologists' view of deep-sea sedimentation patterns from one being dominated by a tranquil ocean with a slow rain of particulate matter to one with episodic but widespread and massive movements of sediment (Stow 1985). Benthic ecologists, in interpreting and reconstructing causes for distributions of deep-sea fauna should incorporate a similar view to that of sedimentologists to better understand how the abyssal benthic fauna has responded to such episodic catastrophes over geologic time. As stated by Einsele et al. (1991, p.14), "...biological responses of benthic communities are...but an integral part of dynamic stratigraphy". The long time scales of benthic faunal succession in the deep sea suggest the importance of turbidity flows as episodic disturbances in determining benthic community structure and, perhaps, in influencing evolutionary processes. Angel and Rice (1996) speculate that turbidity flows, while causing local extinction of benthic communities by burying them, also create mosaics of habitat in time and space that may contribute to the high species diversity of benthic fauna found in the deep sea.

Our analysis of data reviewed in this paper argues for a more all encompassing view of faunal life processes on the abyssal seafloor. One that not only acknowledges the importance of inputs of organic matter from detrital rain, geothermal vents, chemical seeps, organic falls, and various anthropogenic sources, but also inputs from episodic disturbances such as turbidity flows. If viewed as a matrix of dynamical events, the effects of turbidite flows on abyssal fauna occur on larger spatial scales and at longer temporal scales that most other habitat modifications. It is upon these large-scale disturbances that many of the smaller and shorter term effects are superimposed. These effects may be best interpreted from a combined paleontological and neontological approach to the stratigraphic study of deep-sea sediments. Such an approach, as pioneered by Donald Rhoads, has proven useful in comparative studies of fossil and recent shallow-water benthic communities (e.g., Rhoads 1970, 1974; Rhoads & Morse 1971; Rhoads et al. 1972; Rhoads & Boyer 1982; Larson & Rhoads 1983). More research is needed to better understand deep-sea geochemical and biological processes and their interactions in abyssal sedimentary environments as influenced by paleoceanographic events.

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